SOME HABITS AND SENSORY ADAPTATIONS OF CAVE-INHABITING BATS.[1]

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General Introduction.

The present paper embodies the results of about two years of observation on the habits of bats in caves and in the laboratory. The subjects to which special attention has been paid are: The choice of a dwelling; the factors determining times of activity

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and rest; feeding habits; breeding habits; and locomotion, including the sense of direction and means of avoiding obstacles. The senses of direction and means of avoiding obstacles have been investigated experimentally. Studies on the other topics have been carried on largely by observation on free and captive animals.

The work was prosecuted from September 20, 1906, to September 7, 1907, while the author held the Speleological Fellowship in Indiana University with residence at the University's Cave Farm three miles east of Mitchell, Indiana. Later the work was continued in the laboratory of the University at Bloomington, Indiana. There are several caves in the vicinity of both places which are inhabited by a large number of bats, thus affording exceptional opportunities for the study.

Some of the notes, especially those on breeding habits, are very brief. However, it is thought best to include them, together with such facts as those contained in the section on morphological peculiarities, in order to give a more complete idea of the biology of the animals. The experimental studies also need to be continued.

The data presented are in part psychological, but it is the purpose of the present paper to treat it from a biological rather than a psychological standpoint.

The work has been carried on under the direction of Dr. C. H. Eigenmann, professor of zoölogy in Indiana University, to whom I am indebted for constant advice and criticism. My thanks are also due to Dr. Charles Zeleny, associate professor of zoölogy, for helpful suggestions and for aid in revising the manuscript.

Previous Work.

Published observations on the habits of North American Bats are limited to scattered paragraphs in natural histories and taxonomic papers. A number of short papers have been published on English, and a few on Continental European bats. The only extensive studies on the subject are two by Rollinat and Trouessart, the first on the reproduction of the Murine (*Vespertilio murinus*) in 1896, and the second on the sense of direction, in 1900.

Morphological Peculiarities and Relationships.

Bats, constituting the order Chiroptera, are more sharply marked off from their nearest relatives than any other group of mammals. Their closest affinities are with the order insectivora which includes such animals as the moles and shrews. However, the separation is a wide one and no known fossils are in any way intermediate between the two orders.

The most important modification is the adaptation to flight. The changes in structure correlated with the habit of aerial locomotion are the following: The fore limb and pectoral bones and muscles are increased in size and the hind limb and pelvis are reduced. The axis of the hind limb is rotated so that the knee projects backward instead of forward. The digits of the fore limb are lengthened to form a support for the wing membrane. A thin, flexible membrane extends from the sides of the body to the tips of the fingers and from in front of the fore arm to the hind limbs and usually includes the space between the latter and the tail.

Other structural peculiarities are as follows: The carpus is reduced or almost wanting. The first digit (thumb) of the manus is short, nearly free from the wing membrane, opposable, and terminated by a curved claw. The other digits of the manus are long, slender, included in the wing membrane and not terminated by nail or claw. The pes has five short, subequal digits, each with a curved claw. The mammæ are pectoral and there is usually but one pair, although a few species have two pairs. The cerebral lobes are without convolutions, and the cerebellum is relatively large. The ear conch has a slender internal lobule called the tragus in most species, and in several families there are foliaceous appendages of skin about the nostrils.

These structural modifications are worthy of note because they are correlated with the characteristic habits of the animals. Walking or running, after the manner of most animals, is seriously impeded by the lengthening of the fingers, the presence of a membrane joining the limbs, and by the reversal of the direction of the knee flexure. Locomotion on solid surfaces is therefore the rare exception and flight is the common method of progression.

The hind limbs are of use chiefly for clinging while at rest; the fore limbs form only an inadequate support for the animal while at rest and they cannot be used at all for grasping as in most mammals but, as in birds, they are the chief organs of locomotion.

Most insectivorous and carnivorous mammals use the paws to assist in seizing and killing prey and, at times, rest their food against some solid object while eating it. Bats, on the contrary, seize their prey with the mouth, like swallows and flycatchers, and the large, mobile lips assist in holding the food and drawing it into the mouth. They usually masticate it while flying and do not recover any portion that may be dropped.

So greatly has this method of feeding modified the habits of our common vespertilionine bats that the caged animals rarely learn to take food from a dish or from the floor of the cage, although they will eat it readily if it is held directly in front of them.

The expansion of the integument to form the flying membranes has furnished additional surface for bearing organs of special sense and according to Schöbl ('71) a large number of tactile organs are found in the skin of the wing membranes. The nasal appendages and the tragus also have a sensory function, the exact nature of which is not clearly understood.

The nocturnal or crepuscular habit, which is shared by all bats, is doubtless correlated with the increased number of sense organs in the skin which makes the eyes of less importance to the individual and enables it to be active in the absence of light.

Throughout the order there is a relative uniformity of both habit and form. A few species have white markings. In many others the ventral side of the body is paler than the dorsal but otherwise there is a great uniformity of coloration, the prevailing color being some shade of brown. I have seen almost as much variation in the color of a single species from a restricted area as there is in the entire order. While the details of tooth and skeletal structure show that not all the members of the order are closely related, yet the external forms of widely separated groups resemble each other more closely than they do in some of the more nearly related species of other orders.

The Species Studied.

All of the bats found in the United States, except a few species along the southern border, belong to the typical family Vespertilionidæ. In the caves of southern Indiana six species belonging to four genera are found living more or less commonly. In order of greatest abundance they are: The little brown bat, *Myotis lucifugus;* the Georgian bat, *Pipistrellus subflavus;* the Say bat, *Myotis subulatus;* the large brown bat, *Eptesicus fuscus* (*Vespertilio fuscus* of most recent authors); the big eared bat, *Corynorhinus macrotis;* and the large winged bat, *Myotis velifer.* In the literature on the caves of this region, as well as in some of the faunal papers, these species are hopelessly confused. Since the vernacular name, little brown bat, is frequently applied to all of the species except the big eared and large bats, it seems advisable to use the equally convenient scientific names throughout this paper. The observations have been made chiefly on *Myotis lucifugus* but also to a considerable extent on *Myotis subulatus* and *Pipistrellus subflavus.*

These two species of *Myotis* differ chiefly in the size of the ears, the size and shape of the tragus, and some details of cranial structure and dentition. They are about the same size and have the same general appearance and essentially the same habits. *M. lucifugus* is much more abundant than *subulatus.*

Pipistrellus subflavus is much smaller than the other two. It differs from them in color, in the number of the teeth, the form of the skull and other structural details. In habits, it is less active, both in nature and in captivity. For this reason it is not well suited for experiments.

The Physical Environment.

All the more detailed observations on bats in a state of nature were made in the caves near Mitchell. Since the conditions there are fairly typical of the natural environment of the animals elsewhere, a somewhat detailed description will be given. The accompanying diagram (Fig. 1) will serve to illustrate the relations of these caverns and openings but not their proportions. The arrows indicate the direction of the stream.

Five caves open on this tract of land, or rather there is a

single chain of subterranean passages with five openings. These passages are merely a single underground waterway with a good sized brook covering the floor in most places. At two points the roof has fallen in leaving sections of the stream bed exposed.

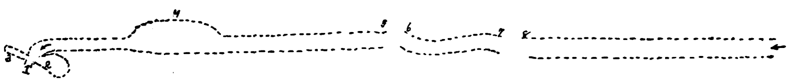

FIG. 1. *1*, Entrance to Shawnee Cave; *2*, lower chamber; *3*, blind passage; *4*, large chamber; *5*, entrance to Lower Twin Cave; *6*, entrance to Upper Twin Cave; *7*, entrance to Lower Spring Cave; *8*, entrance to Upper Spring Cave. Arrows show direction of stream.

These openings have been named as separate caves. The size varies considerably, but the average height is, perhaps, six feet and the width ten. In some places it becomes much smaller and the entire passage is filled with water after a heavy rainfall. In other places the size is much greater, in the large chamber (Fig. 1, *4*) the distance from water level to the top of the chamber is about 40 feet and the width at the widest point about 100 feet. There are numerous lateral passages varying in width from a few inches to several feet. A second large chamber is situated near the extreme lower end of the cave (Fig. 1, *2*).

Temperature records kept for a period of two years, in the large chamber at *4*, show an extreme variation from about 51° F. in January, to 57° in September. The air at this point always contains moisture nearly to the point of saturation. Barometic pressure here varies approximately with the surface pressure although the changes take place more slowly. The physical environment of the cave-dwelling bats during their periods of inactivity, is, therefore, nearly constant for all seasons.

Not less than five hundred bats, representing five species, spent the winter of 1906–7 in these caves. Probably the number was much larger, as only those actually seen were counted and some creep away into the smaller fissures where they cannot be found. These bats come out of the cave to secure food only in twilight or darkness in mild weather.

Since the temperature is relatively constant in the cave throughout the year and there is always total absence of light, the problem which first presented itself was to determine how the

animals happen to come out at the right time. For this purpose daily observations were made on the number, location and movements of bats in the large room (Fig. 1, *2*) near the Shawnee Cave entrance and also near the entrance of the Twin Cave (Fig. 1, *5*), throughout the year, excepting at several times when the cave stream was too high to permit access to these places. The large chamber half way between the Shawnee and Twin Cave entrances was visited weekly during most of the year.

Since this work was begun I have visited one or more times about fifteen other caves, ranging in size from unnamed sinkholes to caverns as large as Marengo and Wyandotte in Indiana and Horse and Mammoth Caves in Kentucky. All of them were inhabited by bats, and in all the approximate number and distribution of these animals have been noted, together with such observations on their habits as it was possible to make. Live bats have also been under observation in the laboratory from time to time.

Bats have resting places but no homes. They never construct any sort of a nest or den nor do they habitually return to a fixed spot at regular intervals, although individuals may have a tendency to resort frequently to the same place. Stone and Cram ('02) state that they appear to hang themselves up wherever daylight finds them. These authors give data which indicate that there may be a periodic return to the same spot at short but irregular intervals.

Of the species found in eastern North Ameria some are habitually cave dwellers and some tree dwellers. The habits of the two groups overlap, however, and at least two of the tree-inhabiting species, *Lasiurus cinereus* and *L. borealis* are known to have entered caves in the past.

I have not been able to obtain a reliable record of either of these species living in the caves of the Mississippi valley at the present time. In the large room (Fig. 1, *4*) of the Shawnee Cave more than two hundred skulls of *L. borealis* and two of *L. cinereus* were found scattered among the rocks on the floor of the chamber. Careful searching in the same and other places failed to discover the remains of more than twenty-five individuals of the three species now most abundant there. The skulls, accompanied

by other bones, were scattered among the rocks in a manner indicating that the animals had probably died where they hung suspended from the roof of the cave and that they had not reached the place by accident nor been killed all at one time by a single catastrophe. The age of the remains is difficult to determine. The cave itself is of comparatively recent origin and the bone deposit is evidently much more recent. However, some of the bones must have been there for a considerable period, since they were covered with a deposit of calcium carbonate more than a millimeter in thickness. The remains may indicate that the red bat is a decadent species, represented by fewer individuals at present than in the past, or they may indicate that it has abandoned the cave-dwelling habit in recent times.

During the summer all of the cave-inhabiting species resort to other places, finding temporary homes in attics, deserted buildings, hollow trees and dark nooks in the forest. Merriam ('87) and Miller ('97) have shown that some of the tree-inhabiting species migrate, and there is evidence that *Myotis lucifugus* does also. Just after most of the bats of this species left the Shawnee Cave, about the end of April, 1907, there was a period during which very few were seen flying about in the evening. A few weeks later they were again seen in abundance. It seems probable that the animals which wintered at this place migrated farther north and that the summer residents had passed the winter elsewhere. Howell ('08), describing the diurnal migration of bats near Washington, D. C., states that some of those observed were small and apparently belonged to the genera *Myotis* or *Pipistrellus*. He further states that more than a hundred bats were seen between 9 and 10 a. m. on September 28, 1907. All were flying with the wind in a southwesterly direction, at a height of from 150 to 400 feet. Their manner of flight was unusually steady and consisted chiefly of a sailing or drifting motion with only occasional zigzag movements.

The number and relative abundance of the different species vary without any relation to the size or physical condition of the cave. Mammoth Cave was visited in November, 1907. In a hasty examination of a part of Little Bat Avenue, about 1,000 bats were seen. These were apparently all *M. lucifugus*. The guides

inform me that they are never seen in the inner parts of the cave — probably not more than a mile from the entrance.

Marengo and Wyandotte Caves were visited in July, 1907. Bats never occur in large numbers in the former, perhaps because a building has been erected over the entrance. On the occasion of my visit two were seen, one of them flying, in Mammoth Hall, the other clinging to the wall in the Pillared Palace. In Wyandotte Cave the bats congregate in enormous numbers during the winter. At the time of my visit in summer only a few were seen. Blatchley ('96) states that they reach the innermost recesses of this cave in winter, but gives no localities at which they were seen beyond Crawfish Spring, about two miles from the entrance. The same authority states that he took 401 bats, by actual count, from a space one by one and seven tenths feet square, on a low ceiling in Saltpeter Cave, Crawford County, Indiana.

In the caves of the Donaldson Farm they have been found throughout all of the explored portions, which, in the Upper Spring Cave, extend more than a mile from any known opening. The smaller caves about Bloomington have been visited at intervals throughout the year. In Mayfield's Cave, four and one half miles northwest of Bloomington, the relative abundance of the two most common species is reversed. Banta ('07) states that *P. subflavus* is fairly abundant while *M. lucifugus* was seen only three or four times during three years' observation of the cave. I visited the place January 11, 1907, and December 21 of the same year, and confirmed his observations, finding 17 of the first species and 2 of the second on my first visit and 22 and 3 respectively at the second visit.

P. subflavus was more abundant also in Strong's Cave one mile from Mayfield's, during the winter of 1907–8. In Truitt's Cave, 2¾ miles from Mayfield's, and considerably larger, there were 40 *P. subflavus* and 51 *M. lucifugus* on November 29, 1907. In Coon Cave, 2 miles from Truitt's and 4½ from Mayfield's, there were about 500 bats on March 29, 1908, not more than 50 of which were *P. subflavus*. Two *M. subulatus* were seen and a few others may have been overlooked; the others were *M. lucifugus*. Eller's Cave, visited on the same day as Coon, was inhabited by about 100 bats. Approximately nine tenths of them were *M. lucifugus* and the remainder *P. subflavus*.

Both of these common species have been seen in some very small caves near Mitchell. In one of these, at least, they seem to have wintered, as several were found there on March 26, and a single *Pipistrellus* was seen under a ledge of rock just outside the entrance in February. This cave is merely an irregularly spiral sink-hole going down to a depth of forty feet but without any large lateral passages. All parts of it receive daylight on bright days and the temperature certainly falls quite low in cold weather.

The other caves mentioned vary in size from the two largest known caverns in North America to small caves with not more than half a mile of passages that are large enough to be explored. The entrance to some of them is a vertical shaft, to others it is a horizontal passage going into the side of a hill.

The conditions prevailing within a cave do not determine a bat's choice of a resting place after it has entered. In Coon Cave, as well as several others that I have visited, there is running water at one point and the air here is usually saturated with moisture. In the upper part of the cave, some distance from the entrance, the atmosphere is always dry and the floor and walls dusty. When I visited this cave, bats were about equally abundant in the dry and in the wet parts. In the latter places the moisture had condensed on the animals and drops of water hung from their fur. The arrangement of hairs is such that this moisture does not penetrate to the skin unless the animal is rubbed in moving about.

Usually the animals go far enough into the cave to be in total darkness and a nearly constant temperature, although as mentioned later (p. 163), they sometimes remain for several weeks where they are reached by both light and cold. Blatchley states that "bats choose as a resting place that part of the roof where small portions have begun to flake, giving a certain degree of roughness, or small crevices, to which they can cling. They cannot attach their claws to a smooth surface, hence from large portions of the roof of a room they may be entirely absent." This statement is partly erroneous, for although they cannot attach their claws to a polished surface, the limestone walls and roof of a cave are ordinarily rough enough to furnish adequate support.

I have frequently found colonies clinging to the roof in places where there were no large prominences and no crevices, and I have seen flying bats secure a foothold in such places in the cave, and also to smooth, but unplaned, lumber in a house. The top and side walls are preferred equally by the different species of *Myotis*, but *Pipistrellus* is generally found on the side walls of the higher chambers. The claws of both feet are hooked about prominences on the stone and when the animal is resting on a vertical wall, the wrist and the nails of the thumbs also rest against the wall and form some support. However, the feet alone are strong enough to support the animal for weeks at a time and even to support several others of its kind when they cling to it.

The social habit is strongly developed in *M. lucifugus*. The large colonies seen by Blatchley in Wyandotte and Saltpeter Caves were almost certainly of this species, although he calls them *M. subulatus*. I have never seen them hanging in clusters as large as these but have frequently seen bunches of fifty or more. The guides at the former of these caves tell me that bats gather there in winter in clusters comparable only to a swarm of bees, and probably equalling such a swarm in number of individuals. *Myotis subulatus* and *M. velifer* are not abundant in this region but are generally found associated with groups of their abundant congener.

Corynorhinus macrotis has only been seen in dim light near the entrances, and there it was found clinging to the side walls with its long ears folded down along the sides of the neck. *Eptesicus fuscus* has not been seen far within the caves nor is it abundant. The largest number I have found in one place is six, taken near the entrance of Mayfield's cave on December 21.

Pipistrellus subflavus is solitary in habit. Occasionally two are found side by side, though I have never seen them clinging to each other except in mating. However, they do not avoid the vicinity of others of their own kind nor other species. This species seems to prefer the side walls of the higher passages. I have never seen it suspended from the roof except where there was a crevice or prominent ledge.

Enemies.

Very few enemies molest bats in their roosting places in the caves. In Eller's Cave I saw evidence that raccoons had been preying on them. It is said that cats have learned to catch the flying bats in Wyandotte Cave. No doubt other carnivora sometimes kill them, but on the whole they are practically free from molestation in the caves. While living in trees they are doubtless preyed upon more frequently. In two instances I have known them to be driven from their roost by birds, once by a robin and once by a blue jay. The barn and great horned owls and the sparrow-hawk have been known to eat them in rare instances.

Their enemies are so few, however, that they have no sense of fear comparable to that of other small mammals. A sharp noise will sometimes startle them into activity. If wide awake they may fly before they can be picked up by hand or net, or if caught they often struggle to get free. But there is never any attempt to "lay low" or to flee from approaching danger. When kept in cages they do not pay the slightest attention to the presence of man, nor try to escape his hand if he attempts to pick them up, even when first brought into captivity. The absence of fear has a marked effect upon the habits and mental life of the animals. Only in such species as are without natural enemies is it possible that there can be such long periods of inactivity or such a deep lethargy in normal sleep.

Periods of Activity and Rest.

Bats are usually active only in the twilight and darkness during warm or moderate weather. The earliest date at which I have seen them flying at a distance from their dwelling place was March 3, 1906, at Washington, D. C. The evening was balmy but there was snow on the ground in places. The latest date I have seen them was November 8, 1906. The evening was warm but had been preceded by some hard frosts. I have seen them come to the mouth of a cave in midwinter and turn back when they felt the cold air. On warm winter nights they no doubt prolong these excursions.

Since they live a part of the time in the caves where there is a total absence of light and where the temperature varies only a few degrees throughout the year, the question has been asked, how do they know when to come out (Blatchley, '96)? The answer is, they try conditions and only come out under favorable circumstances. So far as I know, careful observations bearing on this point have not hitherto been made and it seems worth while to record my own in some detail.

In the first place, hibernation among bats is not strictly comparable to the same process among the lower vertebrates, since it is not one unbroken period of torpor more or less dependent on temperature (Oldham, '05; Rollinat and Trouessart, '96). The vital functions of a frog may be practically suspended during a long period, the lungs and digestive organs almost ceasing to function for the entire winter. In bats the activity of the vital organs decreases, though only to a limited degree. The rate of respiration is difficult to count accurately because the body movement is slight. I have counted the respiration of a dormant bat in the cave at several times during the winter and found the rate to be about 60. At other times I have seen the animals apparently cease to breathe for periods as long as four and a half minutes, and then after one or two convulsive respirations, the frequency would suddenly go up to as high as 82 per minute. I am not certain that breathing actually ceased during the quiescent period but there was no visible body movement. In any case, the same conditions are found during profound diurnal sleep at all seasons of the year.

The animals do not obtain food during the winter but the stored fat is used up and wastes are excreted from the body. Oldham ('05) found fecal matter in the intestine of the lesser horseshoe bat (*Rhinolophus hipposideros*) during the winter and regarded it as proof that the animals had been eating recently. However, fecal matter is, in part, derived from wastes excreted through the wall of the lower part of intestine and is not dependent upon food. The presence of feces is, therefore, no indication that an animal has recently eaten. Lusk[1] states that a fast-

[1] "Science of Nutrition," Graham Lusk, p. 46.

ing dog weighing 30 kilograms excreted 1.88 grams of fecal matter per day. In the large number of bats which I have dissected in winter, the stomach and upper part of the intestine was always empty, although feces were present in the rectum. I am convinced that the cave bats of southern Indiana seldom or never eat during the winter, the stored fat being sufficient to sustain life.

The degree of lethargy bears a close relation to the quantity of superficial fat stored up by the animal and it is not related to the temperature, either without or within the cave, nor to season. In fact, the period of least activity is in the autumn and early winter, before severe weather has begun. The bats are often quite active in the cave during the cold weather of late winter. Between August 8 and September 5, 1907, I took a number of bats, *Pipistrellus subflavus*, *Myotis lucifugus*, and *M. subulatus* from the caves to use in experiments. Some of these were very fat while others were comparatively poor. On September 5 I used two males of *P. subflavus*. The first one was quite poor and flew readily when released in the room after being carried for a short distance in a small box. The second bat had to be prodded and tossed about before it could be awakened from its lethargy sufficiently to fly. Even then its movements were more sluggish and it struck obstacles oftener and also had to be frequently disturbed in order to keep it in motion. I have never seen a bat more difficult to arouse at any time during the winter nor one more torpid when once induced to fly. An examination showed that this animal was exceedingly fat. This is not an isolated case but merely illustrates what has been found several times in this and other species.

When in a state of lethargy, a bat cannot be quickly aroused. Neither noise nor light appears to be a sufficient stimulus to awaken it. Heat will arouse it more quickly than any other stimulus and it will immediately draw away from the heat of a candle. Mechanical stimuli are also effective and bats are sometimes aroused from torpor by being carried for a distance. Merzbacher ('03) found that the reactions of hibernating bats are similar to those in which the cerebral hemispheres have been destroyed. The clinging reflex is very evident, even in the most torpid animals. In the torpid state the body temperature falls

to such an extent that the limbs and membranes feel cold to the touch. As the animals are aroused, the breathing becomes stronger, the temperature rises, the eyes open and often there are convulsive movements of the limbs. The animal may also begin to chatter and to creep slowly. If laid on its back it slowly rights itself. However, it is some time before it gains full control over its muscles. If dropped, the wings spread reflexly, but the animal cannot at once fly. There are intermediate stages of lethargy in which the torpor is less extreme and the animal very quickly gains power over its body, but the extreme conditions described above have been observed in every month of the year except May, June and July, during which months but few bats have been under observation.

Observations on periodic movements of bats were made chiefly at two points in the caves at Mitchell, in the large chamber (Fig. 1, 2) at the right of Shawnee Cave, and at a point about 100 feet within the Twin Cave entrance (5). Both points are so near the entrance that the temperature varies considerably. On bright days a diffuse light reaches both points for an hour or more when the sun's rays fall directly into the mouth of the cave. Daily observations were recorded from January to April, 1907, with the exception of several times when high water prevented entering the cave.

On January 2, with a maximum temperature of 50° F., there were 75 bats at the place of observation in the Twin Cave. A period of low temperature followed, and high water prevented further observations until January 25, when the number had decreased to 9. The number now increased gradually until February 7, when there were 51, although the temperature remained low. With the average temperature slightly rising, the number of bats diminished during the next two weeks to 42 on the twenty-first of the same month. During the next four weeks the number of bats again increased until on March 20 there were 101. The temperature had been rising gradually and with some fluctuations, and the average daily temperature on March 20 was about 45°; a further rise to 70° on March 27 followed. With these higher temperatures the number of bats on the twenty-eighth of that month was only 18. Unseasonably

cold weather during April was accompanied by an increase in bats which reached a maximum of 153 on April 20. Observations carried on during the same period at 2 (Fig. 1), which is another part of the same cavern, showed a variation in the number of bats near the entrance which almost exactly paralleled that in Twin Cave, thus showing that the movements had some common cause and were not wholly accidental.

Apparently the movements have a definite relation to season and temperature. The bats come to the mouth of the cave at intervals throughout the winter, but these intervals are longer in the early winter when the animals are fat and well nourished. The unusually warm weather prevailing early in January may have acted as a stimulus for them to remain near the entrance; no doubt some individuals left the cave at night in search of food. Cold weather followed and the cold, entering the cave, drove the animals back to the warmer parts. However the hunger stimulus was becoming stronger and the bats came to the entrance more frequently and tended to remain there. The maximum number was reached with a moderate temperature, and when the weather became quite warm the animals left the cave and did not all return but found temporary homes in trees and buildings. Cold weather in April brought them back to the cave again, but most of them remained near the entrance. When the weather again became warm at the end of April, they left the cave for the summer.

Other observations were made on the movements of individual bats at different times. The location and orientation of different individuals were carefully marked and the place was visited weekly. Out of 18 bats observed between November 19 and December 3, 14 had moved within one week, and none remained in the same place during two weeks. Later in the winter one bat remained in the same spot near the entrance from February 4 to 27. Light reached the spot throughout the day and the temperature remained near freezing point for several days at a time. However, this was an exceptional case, as not many bats remained in one location for more than four or five days during the latter part of the winter. The small bat, *P. subflavus*, is less active. Its average period of staying in one place is about two weeks, and one was noted in the same spot for 44 days.

Data on the daily movements of bats are still very meager. Moffat ('05), who has observed Irish bats, states that among the Irish bats, Daubenton's, the pipistrelle, and the long-eared fly all night. The Noctule flies in the evening twilight, and the hairy-armed flies for about an hour shortly after sunset, then retires to its roost and again comes out shortly before sunrise. Six pipistrelles, living solitary, were found to have similar, and very regular habits, leaving the holes in hollow trees from ten to thirty minutes after sunset, and returning from forty to eighteen minutes before sunrise. The observations, which were made in August, showed that there was no difference for warm nights and raw, cool nights. Morao ('63) states that the bats in an immense colony of *Myotis lucifugus* in the attic of a house near Charlestown, Maryland, were accustomed to leave their roost twice in one night. His somewhat poetic statement that they left at "the call of the whip-poor-will" cannot be considered accurate, for in such a large colony, individuals could not be noted and any general disturbance of the colony might be mistaken for a renewal of the activity of the individuals.

The same difficulty exists with regard to determining the daily activity of bats in a cave. Their dwelling place is so large, and the possible exits usually more than one, so that their movements cannot be watched. It is possible to go into the cave and examine individuals, but there is the danger of disturbing them and causing them to leave sooner than they would if unmolested.

I have seen bats flying in the cave at all hours of the day and night, and have also found them at rest there at all hours. Evidently they may awaken from sleep at any time and fly to the mouth of the cave. If the temperature and light are favorable they go out and search for food. If it is cold or if the light is too strong, they go back. If they are fat and well nourished they settle down to another more or less prolonged period of lethargy. But if the hunger is strong they are apt to remain awake and active, or only go to sleep for a short time.

The bats in the clusters seen in spring or late winter were usually awake and chattering. In the fall and early winter bats are generally isolated and torpid. Those that are active are very apt to reach the mouth of the cave as soon as conditions out of

doors are favorable for their activities. The presence of bats in the cave at night, when others are out searching for food, shows that there is no definite time at which they all leave their roosts. This fact has also been observed with regard to the European pipistrelle (*Pipistrellus pipistrellus*) by Whitaker ('07), who says that only part of a large colony left their roost under a roof on a certain night. If a large percentage of the animals does become active at about the same time, it must be remembered that many of them pass the summer in places where daylight reaches them and the absence of light as night falls may be a direct stimulus to activity. Falling temperature at sunset may also stimulate the animals to activity when they are not in the caves.

On rare occasions the hunger stimulus may be so strong as to overcome the natural repugnance to light, and the animals come out to search for food in daylight. I have witnessed this but twice. In late autumn a *Pipistrellus* was seen circling high above the trees, and at another time, May 9, 1907, a *Myotis lucifugus* was seen feeding in the bright noonday sun near the mouth of Shawnee Cave.

On the average, a bat certainly does not fly more than six hours out of twenty-four, and that for not more than eight months of the year. At least five sixths of its life is spent hanging head downward in the dark.

From the foregoing facts we may assume that a bat's life is made up of a series of alternating periods of torpor and activity. The relative and absolute length of these periods depends on the state of bodily nutrition.[1] When the body is well nourished and the quantity of reserve fat large, the periods of lethargy are long and the time of activity short. As the stored fat is used up the periods of lethargy become shorter and active states longer and more frequent. During the season of greatest activity, from May to July inclusive, the times may correspond to daylight and darkness, and the condition of the animals to ordinary sleep and activity. However, the longer periods have no direct relation to

[1] The physiology of hibernating bats has been studied by Rulot ('02) and Merzbacher ('03). According to the former, glycogen and albumen are consumed during hibernation, especially toward the end of the period. It is evident that the hibernating state in the bats studied by these authors is more profound than it is in the bats which I obtained in the caves.

season or temperature nor are any of the periods dependent upon the physical environment.

Feeding Habits and the Perception of Food.

The feeding habits of bats are by no means easy to study. They habitually secure their food while flying, and then only during twilight or darkness when it is impossible to distinguish their movements accurately. In a state of nature their food consists largely, perhaps wholly, of insects. The single time that I have seen a bat feeding in daylight near enough to distinguish its prey, it was catching small ephermerids and diptera. At dusk they can sometimes be seen pursuing larger insects, apparently beetles. The food is so thoroughly masticated that examination of stomach contents furnishes no definite clue to the identity of the things eaten. Neither does the food that an animal will eat in captivity afford an index to its natural food. Meal worms seem to be the favorite article of diet of captive bats. Fresh meat is eaten readily. They will also eat a small worm (*Tubifex*) which lives only in mud and certainly is never eaten by the animals in nature and has not been by their ancestors since the flying habit was acquired.

Dobson ('78) states that a fruit bat (*Cynopterus*) which he captured in Calcutta consumed a banana twice its own weight in three hours. Whitaker[1] states that the hairy armed bat, *Ptergystes leisleri*, eats about five dozen meal worms a day, and that a female noctule, *P. noctula*[2] after several days fasting, during which she gave birth to young, consumed eight dozen meal worms in one evening. None of the bats which I have had in captivity have been voracious eaters. Captive bats will learn to eat meal worms greedily when they are offered to the animal with the fingers or a pair of forceps. Only on one or two occasions have I ever seen a bat pick up food from the floor. When a meal worm is taken between a pair of forceps and held before a bat, the animal will snap at it eagerly, especially if the worm is wriggling. However, its efforts are not well directed and it is as apt to get the forceps in its mouth, or to miss the objects completely, as it is to seize the worm.

When food is accidently dropped the bat does not make any

[1] '07. [2] '05.

attempt to recover it and does not even turn its head to look for the lost morsel; generations of flying ancestors have not found it advantageous to try to recover an object dropped while on the wing.

Bats are not wholly dependent on a single sense for distinguishing their food. Smell, on which many other mammals are chiefly dependent, here is of subordinate importance. The reason is to be found in the way in which food is secured. Any creature walking on a solid surface and having a characteristic odor, can be located, or can be traced some time later, by an animal with a keen sense of smell. But flying insects, which form the chief food of bats, do not leave a permanent odor in their path nor can their presence be definitely localized because the odors are diffused too rapidly and unevenly by shifting currents of air. I have held meat, meal worms and insects near a hungry bat and it did not seem to notice their presence until some sense besides smell was stimulated. However, fresh meat fastened to the side of the cage was found and eaten after a time. On one occasion a bat that was running across the floor of a cage perceived a piece of meal worm it was passing and picked it up. This was, however, the only instance of the sort I have observed in handling and feeding a large number of bats. The same animal and others seemed quite unable to find meal worms or insects lying quietly on the bottom of the cage. Occasionally they found meat placed in a small dish. This happened more often with *Eptesicus* and *Pipistrellus* than with either species of *Myotis*, though the latter found the meat more readily when it was fastened to the side of the cage so that the animals climbed about over it.

It must not be inferred from the above statements that the sense of smell is lacking, or even rudimentary. All bats have a strong odor, the purpose of which is probably to attract others of their kind. This may be taken as an indication that smell is well developed, for otherwise the odor would be useless. The action of the animal mentioned above in stopping to pick up the meal worm, and the ease with which others learned to find and eat such unfamiliar food as meat, also indicate that the sense of smell is not lacking. The fact that they do not usually notice food when it could be perceived by this sense alone, indicates only that they are not accustomed to find it in that way.

After extended observations on the subject, I am still unable to form any definite conclusions with regard to the importance of sight to these animals. That they can see light and darkness and moving objects is unquestionable. That the sense of sight is not highly developed is equally certain. The behavior of some of the animals appears to indicate that at times they depend on this sense to a considerable degree, both in securing food and in avoiding objects.

On bright nights, and in twilight, a dark, moving object can be readily seen against the skyline. Under such circumstances sight would be of use to bats in helping them to find the general location of food. Whether it really guides them at such times is a point not yet determined.

Bats are extremely sensitive to vibrations of high frequency. A sharp whistle, sucking noises with the lips, tearing a sheet of paper and drawing the finger nail across a piece of thin board or rough cardboard cause them to start violently, but low pitched, rumbling noises have no apparent effect.

Flying insects usually produce a high-pitched hum. While it would be of advantage to a bat to perceive these sounds, the evidence that they are actually guided to their prey by hearing them is inconclusive. It is not possible in observations on feeding to distinguish between response to hearing and to tactile stimulation, by the vibrations. The voice of different species of bats varies but it is always high pitched. Alcock ('99) states that the voice of the hairy-armed bat has about 17,000 vibrations per second. The pitch has not been determined for the voice of the American species.

It is evident, however, that it is the *motion* of the insects that lead to their perception by bats. Whitaker ('06) states that a noctule which he observed caught a pebble tossed into the air. In this country boys often gather under the electric lights or at the edge of a wood where bats are abundant in the evening, and knock them down with a fishing pole waved rapidly in the air. In both cases the bats are attracted by the moving object and probably by hearing. The tactile sense, located in the vibrissæ and lips, is certainly very delicate and doubtless aids the animal to definitely locate its food. In feeding meal worms to bats I

have found that the animals do not, as a rule, pay any attention to worms held near them so long as they are quiet. But when the worms begin to wriggle the bats at once become excited and begin to snap at them. This happens when they are not touched by the worms and when the latter are out of the range of vision. It seems improbable that touch is the sense here aroused. The food must have been perceived by the tactile organs being stimulated by air currents set in motion by the moving worms.

It is said that bats use the interfemoral membrane, which the flying animal carries curved downward and forward under the body, as a sort of scoop in which insects are caught. It is possible that food is thus secured at times, but it is more often seized in the mouth. However, the membrane is used as a pouch into which the bat thrusts its head when it has an insecure hold on an insect. The membrane thus serves as a pouch to prevent dropping the food and also serves as an object against which the struggling prey can be pressed while a firmer hold is being secured.

Observers (Whitaker, '06; Grabham, '99), who have studied the habits of various European species of bats agree that they drink while on the wing, flying over a body of water and dipping down to its surface to drink. I have observed the same habit in *M. lucifugus;* it probably alights to drink also. When in captivity this species learns readily to come to a small cup of water placed on the floor of its cage. The animal gets up on the edge of the dish, resting on its wings and body and bracing with its feet. Often it dips a part of the forearm and wing into the water. The lower jaw and tongue are thrust in, the mouth is filled with water and, generally, but not always, the head is raised to its normal position and the water is taken down in a succession of rapid swallows. On the whole, the method of drinking resembles that of a young chick, except that the head is not lifted so high.

If the conclusions given above as to the manner of perceiving food are correct, it is obvious that water must be perceived in some other way, since it is obtained where it is relatively stationary and noiseless. On two occasions I have seen bats in the laboratory apparently attempt to drink while flying. On the first occasion there was an aquarium of running water in the room. The bat

flew near enough to this to feel the splashing water and then turned and flew repeatedly across the room, keeping near the floor and frequently giving the floor an audible bump with its opened lower jaw. The other time there was no running water in the room which could have set off the impulse, but there was standing water which it may or may not have approached. On both occasions there was a good light, either artificial or daylight, and the floor was of a dull, yellowish brown color which might look to an animal flying over it like water of a pond on a starlit night.

The evidence at hand is not sufficient to prove the point, but it seems probable that sight may be the sense by which water is usually distinguished, but that moisture-laden air, rising from a body of water to a bat flying above it, also helps the animal to locate water.

I am unable to say whether bats ever drink in the caves. In most places there is so much moisture that they probably do not become thirsty. There is no evidence to show that they ever eat in the caves. Some insects could be obtained there but the quantity would be inconsequential as compared with the number of bats to eat them. The lack of sufficient food is doubtless the only reason that they have never become true cave dwellers.

Locomotion.

Bats are more helpless on their feet than most birds. This is in part due to the mechanical impediment of the flying membrane, and in part to the skeletal modification outlined in the section on morphological characters. As a result of these changes in form the animals cannot support themselves on their hind limbs alone, as do birds and man, nor can they rest upon the terminal part of the fore limbs. When walking upon a horizontal surface a bat rests upon the sole and claws of the hind foot and upon the carpus and thumb of the fore limb. The phalanges are usually folded backward along the fore arm, as when at rest, though the wing is sometimes slightly expanded. The tail and interfemoral membrane are curved forward under the body and both the tail and the wing may touch the floor at times. The body is elevated so that it clears the floor. The limbs are moved as in other

mammals, the right hind limb being lifted with the left fore limb, and vice versa. The steps are necessarily very short because the membranes prevent long steps, although they are sometimes quiet rapid. This rapid movement across the floor has been very well described as "scurrying." It is never kept up for a long distance. The animals apparently become tired in a run of a few yards.

Flying is the usual mode of locomotion for bats and they have the capacity for flight developed to a high degree. We have no definite information as to the speed of a flying bat, the duration of its periods of flight, nor the distance that it will travel from either its birthplace or its temporary dwelling. Some of the animals that I have had in captivity seemed to tire very quickly and could not be easily induced to take to flight when they had once settled down. Attempts to estimate their speed can be scarcely more than a guess because their erratic, wavering flight is much more difficult to measure than that of a bird, and because of their nocturnal habits. *Myotis lucifugus* probably flies at a rate of about ten to twelve miles an hour. *E. fuscus* flies faster and *P. subflavus* not so fast. The flight of the last named species is weak and wavering and resembles that of a butterfly. *E. fuscus* has a relatively rapid, strong and steady flight, while *Myotis lucifugus* and *M. subulatus* are, in a way, intermediate between the two.

The quick turns and evolutions which bats make as they fly about in the twilight are for the purpose of catching flying insects. However, their manner of flight is essentially the same when they are not feeding. It may be that this erratic flight has some relation to the kind of place in which these animals are accustomed to live. In the earlier stages of the evolution of flight, bats must have lived in trees and their movements must have consisted of short leaps or flights among the branches, where skill in avoiding the limbs and in clinging to them was of more consequence than steady or prolonged flight. As the power of flight became better perfected the animals would still secure their food largely among the trees, but would remain on the wing longer and would dart here and there among the branches snatching food as they went. Hence the importance of being able to readily perceive and avoid small objects. The cave-dwelling habit would tend to further develop

these peculiarities, since the angles and projecting ledges of the caves would prevent a straight and continuous flight. Catching insects on the wing would make agility count for more than endurance and steadiness, and hence the characteristic mode of flight has been preserved.

The migrations previously mentioned (p. 155) would seem to indicate that individuals may travel five or six hundred miles twice a year. The steady flight noticed by Howell ('08) in diurnal migration may be taken as an indication that these animals make long, continuous flights and have considerable endurance. In this characteristic we find another analogy to birds.

A flying bat can change its course or check its momentum very quickly. When it does not perceive a solid object that it is approaching, it sometimes strikes its head while going full tilt and falls down. Usually, however, an object is perceived before actual contact takes place, and in that case the animal is always able to check its flight and alight on the obstacle if it is too near to turn aside and avoid it.

The quick turns and dodges seem to be made by changing the angle of the wings either antero-posteriorly or dorso-ventrally. The interfemoral membrane and tail may act as a rudder, but a bat from which they had been removed flew as well as before the operation.

A flying bat can alight on a vertical wall in several different positions. Oldham ('05) states that the British Vespertilionidæ alight on vertical surfaces with the head upward and reverse quickly after obtaining a foothold, while the lesser horseshoe bat (family Rhinolophidæ) reverses in the air and alights head downward. Both of our common species of *Myotis*, and I think all of our other cave-inhabiting bats, can reverse in the air and alight head downward although they do not always do so. When flying against a window screen or some other object, not perceived until it is almost touched, they alight head up, striking with the anterior end of the body first and letting the posterior end settle down.

The reversal consists in a sidewise dip with wing and head, the hind limbs being brought forward and thrown upward at the

same time so that the one wing is directly above the other; the sidewise motion then continues far enough to bring the head under the tail and the claws of the feet grasp the surface. If the wall is too smooth to furnish a foothold the bat is in position for immediate flight. Sometimes the position is only partially reversed and the animal alights sidewise. In this case the thumbs support most of the weight.

A flying bat can secure a foothold upon a horizontal surface beneath which it is flying as easily as on a vertical wall. To secure a foothold the bat throws its head downward and its feet upward and forward till they touch the roof and the claws grasp the supporting object. The quickness with which the momentum of flight is checked is one of the nicest adaptations of a bat's life. Only a slight roughness is necessary for the sharp curved claws to secure a firm hold. I have seen a flying bat clasp and hold a vertical number 16 wire that it accidentally struck. The fore arms were placed behind the wire which was pressed against the back as a man might hold a cane thrown across his shoulders. A bat in flight can catch a rafter or similar object by a single thumb, or by the claws of one foot. Metal, glass, polished wood or stone are not rough enough to furnish support, but unplaned boards, and rough limestone, furnish adequate foothold.

When a bat launches into flight from a perch on the roof or side wall, it always drops downward, spreading the wings as it drops. It can launch into flight from the floor or other flat surface, but it cannot rise vertically in the air from a resting position. A bat which fell into an empty aquarium, 16 inches in diameter, and the same depth, was unable either to climb its smooth sides or to fly out of it. When caught in a dip net they are unable to fly out of it, but must climb the sides and fly from the rim to escape, a fact which makes it easier to capture them.

Breeding Habits.

The reproduction of some of the European bats belonging to the families Rhinolophidæ and Vespertilionidæ has been studied by several zoölogists. Benecke ('79), Eimer ('79), Van Beneden and Rollinat and Trouessart ('96), all state that copulation takes place in late summer or autumn. The spermatozoa fill the lu-

men of the uterus and remain alive but inactive throughout the winter. Ovulation and fertilization take place at the return to active life in the spring and development begins at once and continues without a resting stage. Duval ('95) states that bats copulate a second time immediately after hibernation, but Rollinat and Trouessart ('96, p. 220) consider his observations to be erroneous.

The reproduction of American bats has not been studied in detail. I found *Myotis lucifugus* copulating in Shawnee Cave on October 27, 1906, and at two unrecorded dates shortly afterward. In Truitt's cave I saw a pair copulating on October 19, 1907. Two pairs of *Pipistrellus* were apparently copulating in the same cave on November 29, but they were too high to be reached and I could not be certain. A pair of *Myotis subulatus* appeared to be copulating early in April, 1907, but they also were in a position where they could not be obtained or be carefully watched. If mating actually took place at this time it may have been the post-hibernal mating mentioned by Duval, as it is extremely improbable that this species would copulate at a very different season from its near relative.

In sexual congress the female clings to a vertical wall or ledge. The male attaches himself to the posterior part of the body of his mate, and clings to her fur and membranes with his claws, but also rests in part on the interfemoral membrane and body. The posterior portion of his body is flexed forward, pushing aside the interfemoral membrane of the female, so that contact between the genital organs can take place. Coues and Yarrow ('75) state that the red bat (*Lasiurus borealis*) copulates during flight, but this statement is so at variance with the facts observed for the other species that it cannot be accepted without further confirmation.

The uterine contents of *M. lucifugus* were not examined to determine at what time fertilization takes place. However, embryos were not present in any that have been examined in the caves, including several as late as April 9, and one on April 27. It can be asserted, that in this species, development does not begin until the beginning of the summer activity of the female. After this time the females seldom or never enter the caves and I have

not been able to find them at all during the period of gestation and the rearing of the young, nor have I ever found the young bats of either species of *Myotis* before they had reached adult size.

Pipistrellus likewise leaves the cave for the breeding season, although I have taken a female of this species containing three small (about 2 mm.) embryos in the Twin Cave on June 6.

The males of certain oriental species of bats (*Chiromeles torquatus* and some of the species of *Cynopterus*) have special adaptations for carrying the young. The Standard Natural History (p. 161) generalizes from this fact so far as to say that "it is not doubtful that the male attends to his mate and young with considerable assiduity." The absurdity of this statement in so far as it applies to our common Vespertilionidæ, is apparent from the further statement on the same page that "the sexes do not mingle and come together only at the nuptial season." There is almost certainly no permanent mating but the animals copulate indiscriminately, several males perhaps mating with one female. This is what might be expected in gregarious animals that do not rear their young in a nest or den, but give birth to them at any convenient place and carry them about. Rollinat and Trouessart ('96) believe that this is what happens in the case of *Pipistrellus pipistrellus* and *Vespertilio murinus*.

The females of our species of *Myotis*, and perhaps the other Vespertilionidæ of eastern America, probably seek out isolated places in which they give birth to the young and where they spend most of the time while rearing them. As long as they remain in the cave in the spring there is no complete segregation of the sexes. I have found the two sexes associated in Twin Cave on different dates in April (the latest examination was made on April 25) both in the years 1907 and 1908.

The females leave the caves somewhat earlier than the males. On April 25, 1908, in a search through the outer parts of all the caves on the Cave Farm, I found 23 male *P. subflavus* and 4 females. Twenty-five male *M. lucifugus* were also found, to only 2 females of that species. On May 13, in Truitt's Cave, there were 17 *P. subflavus* and 5 *M. lucifugus*, all of both species being males.

The Behavior of Bats in Captivity.

Bats in captivity, as well as those at liberty, are very erratic and uncertain in their behavior. Some of them are sluggish and cannot be used at all for experimentation. Others are quite active for a time and then suddenly retire to some corner, hang themselves up by the feet, and do not move from their chosen position for hours, or even days, unless they are disturbed. If disturbed, they sometimes open their mouths and chatter angrily, but do not move unless forcibly pushed aside. Others will fly a short distance and then settle down again. Occasionally a repeated disturbance will arouse them to complete activity.

They learn to go and drink from a small dish of water placed in their cage. Some have learned to go to a dish of raw meat and eat. As a rule, however, they do not find food on the floor of the cage, but will eat more readily if meat is placed on the sides, where their head comes in close contact with it as they move about.

Insects are not readily eaten unless presented to them with fingers or forceps. Meal-worms are eaten with much apparent relish, but often, especially in winter, even this food has to be thrust into their mouths so that they will taste it before they learn to eat. I have often turned the meal-worms loose in a cage or small box with bats, but not one has ever been picked up as it was crawling around, although they sometimes crawl over the animal's body and membranes.

The manner of eating, and the time required for the consumption of the same amount of food, varies considerably at different times and with different individuals. They eat slowly as compared with other animals of equal size; from one to five minutes being required for eating a single meal-worm. Some swallow only the juices and soft parts, letting the chitinous shell pass out of the corners of the mouth.

During the winter 1907–8 my captive bats were kept in small glass and wire cages that were placed in a small photographic, dark room. The door was never closed tightly, except temporarily, so the darkness was not complete and ventilation was fairly good. The temperature varied somewhat but never fell below 40° F. nor rose above 65°. The animals spent most of

the time clinging to the sides of the cages near the top, but went down now and then to get water. As long as they were undisturbed they moved about little and remained in good health. Some *M. lucifugus* obtained in Mammoth Cave, November 8 were kept alive until March 26. When taken out and held in the hand or placed in a warm room and touched occasionally, their temperature gradually rose, and in from ten to fifteen minutes they usually began to creep about, and then to fly. For some reason that I have not discovered, the animals never lived long when they were disturbed frequently. From February 10 to March 3 was the longest that I was able to keep a bat in good health when using it daily for experiment. It is possible that the dry atmosphere of the steam-heated rooms is not suitable for them.

A characteristic of bats, liberated in a large room where they can fly about, is the tendency of an individual to alight frequently in the same place.

Another noteworthy tendency is that of exploring every nook and corner of a room. It results in finding any crevices through which it is possible to escape. This tendency must have been of incalculable importance to animals accustomed to spending much of their time in dark retreats, reached only through small and winding passages.

(*To be continued.*)